TAXONOMY AND GEOGRAPHY OF *NICOLLETIA* (COMPOSITAE: TAGETEAE)

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Nicolletias are easily distinguished from other Tageteae by pinkish to magenta stripes or bands on the laminae of the white to pink ray corollas, a peculiar pappus of fascicles of coarse bristles alternating with and subtending lanceolate, awn-tipped squamellae, and, apparently, a novel chromosome base number, $x = 10$. Geographic ranges of the three species are allopatric and each is restricted to a single floristic province (Fig. 1): *Nicolletia edwardsii* in Chihuahuan Desert, *N. occidentalis* in Mojave Desert, and *N. trifida* in Sonoran Desert of Lower California.

Position of *Nicolletia* within Tageteae is puzzling. Morphologically, its nearest relative is *Leucactinia* Rydb., a little known monotype with white to pale yellow ray corollas, a pappus of coarse bristles (the innermost sometimes narrowly hyaline-margined at base), and chromosome number unknown. *Leucactinia* is known from only five localities in Nuevo Leon, Coahuila, San Luis Potosi, and Aguascalientes. Isolation of this pair of genera within Tageteae probably reflects an early derivation from ancestral Tageteae (Strother, 1977).

CHROMOSOMES

All species of *Nicolletia* have been reported to have $2n = 10$ II in four to six populations of each. The base chromosome number for the genus is taken to be $x = 10$. Base numbers for other genera of Tageteae are: 7, 8, 9, 11, 12, 13, and 15; base numbers of seven of the 16 genera remain unknown.

One population of *N. trifida* (30 miles south of San Filipe, *Powell and Turner 1739*, DS, NY, US) has been reported to have $n = 20$. Additional counts of $2n = 10$ II from *N. occidentalis* are reported here: CA, Los Angeles Co., ca. 11 and 12 miles east of Palmdale, *Strother 1221* and *1222*, UC.

TAXONOMY

NICOLLETIA A. Gray in Frémont, Rep. exped. Rocky Mts. p. 315. 1845. Type: *Nicolletia occidentalis* A. Gray.

Annuals or perennial herbs; stems spreading to erect, 5—30 (—50) cm high at anthesis; glabrous, often glaucous. Leaves mostly alternate (lowermost opposite); pinnately divided into 3—9 (0—11) stout to linear-filiform lobes, these usually bristle-tipped and bearing a subterminal, orangish, pellucid gland containing strongly scented oil. Heads terminating branches, subsessile or pedunculate. Involucres turbinate to fusiform or campanulate; 12—18 mm high. Calyculus of 0—6 short, lanceolate to triangular bractlets.

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Phyllaries 8—12; free to base; imbricate; membranous, narrowly scarious-margined; most bearing 1—5, oval to linear, pellucid glands; persistent and becoming reflexed. Receptacle convex to hemispheric or conical; favose to alveolate; sparsely and minutely hispid to glabrous. Ray florets 8 (7—12); pistillate, fertile; corollas white to pink, laminae usually with bands or stripes of magenta or pink, very showy, apically retuse or shallowly 3-lobed. Disc florets 15—100+; perfect, fertile; corollas pale to bright yellow, sometimes tipped with purple, narrowly cylindrical, 7—9 mm long, tube much shorter than the throat, lobes 5, deltoid to lanceolate; anthers minutely sagittate; style branches long, slender, tipped with filiform, hispidulous, astigmatic appendages. Achenes slender, somewhat clavate, blackish, closely pubescent with short, white to rufous hairs. Pappus of 5 (—6) fascicles of 7—15 fine to coarse, hispidulous bristles subtending and alternating with 5 (—6) lanceolate, awn-tipped squamellae.

Key to *Nicolletia*

a. Leaves mostly 3—5-lobed, rachis scarcely wider than lobes; laminae of ray corollas 7—16 mm long; disc florets mostly 15—50 per head.
  b. Leaf lobes mostly patent; peduncles 5—30 mm long, heads held scarcely above foliage; laminae of ray corollas mostly 9—16 mm long; Chihuahuan Desert. . . . . 1. *N. edwardsii*
  bb. Leaf lobes mostly antrorse; peduncles 10—70 mm long, heads held well above foliage; laminae of ray corollas 7—11 mm long; Lower California. . . . . 2. *N. trifida*
aa. Leaves mostly 7—9-lobed, rachis mostly 2—3 times as wide as lobes; laminae of ray corollas 4—8 mm long; disc florets mostly 60—100+ per head; Mojave Desert. . . . . 3. *N. occidentalis*

1. NICOLLETIA EDWARDSII A. Gray, Smithsonian Contr. Knowl. 3(5):119. (Pl. wright. pt. 1) 1852. Type: Mexico, Chihuahua, "near Guajuquilla" (present Cd. Jimenez, near 27°N, 105°W), Aug, *Dr. Edwards s.n.* Holotype: NY!

Annuals (or short-lived perennials); spreading, mostly 5—25 cm high, weakly succulent, sometimes weakly glaucous. Leaves 1—6 cm long, pinnately parted into 3—5 linear to filiform, usually patent lobes (or simple and filiform), sometimes with additional short, lateral lobes. Peduncles 5—15 (—30) mm long, heads held scarcely above foliage. Involucres narrowly turbinate to weakly fusiform. Calyculus of 4—6 triangular bractlets 1—2 mm long. Phyllaries mostly 6—8, lanceolate, acute to attenuate, 11—15 mm long, 2.2—4.1 mm wide, membranous, hyaline-margined, each usually bearing 1 subapical and 2—4 submarginal, linear pellucid glands. Ray florets 8 (7—9); tube of corolla slender, 4.2—6.2 mm long; laminae linear to narrowly elliptic, 7—16 mm long, 3—6 mm wide; style branches exserted 0.1—1.1 (—2.2) mm. Disc florets 15—25 (—50); corollas creamy yellow, 7—8 mm long, tube 1.5—1.7 mm long, throat narrowly cylindrical, ca. 5 mm long, lobes 0.4—0.7 mm long, deltoid to lance-triangular, papillose and sparsely glandular-puberulent; anthers ca. 3.5 mm long, including basal collar (0.3—0.4 mm long) and apical appendage (0.4—0.5 mm long); style

branches 2.5—2.7 mm long, including appendage (1.7—2.2 mm long). Achenes 5—7 mm long. Pappus bristles 3—5 mm long; squamellae 4.8—7.2 mm long, including awn (1.8—3.3 mm long).

Distribution (Fig. 1): Chihuahuan Desert from trans-Pecos Texas south and east to northern Zacatecas. Locally common to abundant on sandy to silty, often calcareous or gypseous, soils on flats or playas in *Larrea* Scrub; 800—1650 m. Flowering mostly Aug—Oct, following summer rains; occasional through the year (Fig. 1).

2. NICOLLETIA TRIFIDA Rydb., N. Amer. Fl. 34:180. 1915. Type: Mexico, Baja California, Bahia de los Angeles (ca. 29°N, 113°35′W), Apr—Dec 1887, *E. Palmer 569*. Holotype: NY!; isotypes: GH!, NY!, UC!, US!

Annuals or short-lived perennials; ascending to stiffly erect, 1—3 (—5) dm high, often succulent and glaucous. Leaves 3—5 (1—7) cm long, pinnately parted into 3 (0—5) linear-terete, antrorse (30—45°) lobes. Peduncles 2 (1—7) cm long, heads usually held well above foliage. Involucres narrowly turbinate to somewhat fusiform or campanulate. Calyculus of 0—2 lance-triangular bractlets 1—2 mm long. Phyllaries 8 (7—10), lance-linear to oblanceolate, attenuate or abruptly acute, 12—16 mm long, 2.5—3.8 mm wide, very thin, hyaline-margined, each usually bearing a conspicuous subapical gland and, rarely, with 2—4 lateral, linear glands. Ray florets 8 (—11); tube of corollas 4.8—6.5 mm long; laminae ovate-elliptic, 7—11 mm long, 2.5—5.2 mm wide; style branches exserted 0.8—2.2 mm. Disc florets 30—50 (—80); corollas yellow, 7.2—8.9 mm long, tube 1.8—2.7 mm long, throat 4.5—5.1 mm long, gradually dilated, lobes 0.9—1.1 mm long, narrowly triangular, papillate, not glandular-puberulent; anthers 3.5—3.9 mm long including collar (0.4—0.6 mm long) and apical appendage (0.6—0.8 mm long); style branches 3.1—3.8 mm long, including appendage (1.1—1.5 mm long). Achenes 5—8 mm long. Pappus bristles 3—6 mm long, very fine; squamellae 4.2—7.7 mm long including awn (0.7—2.2 mm long).

Distribution (Fig. 1): Sonoran Desert portion of Lower California between 24° and 30°30′ N; 0—1300 m. Flowering mostly Feb—May and Oct—Nov, following rains; occasional through the year (Fig. 1).

Achenes of *N. trifida* seem eminently suited for disperal and much of western Sonora and the islands of the Gulf of California seem to provide ample hospitable habitats, yet *N. trifida* has been reported from only one of the islands (Isla Inez, very near the coast of Baja California Sur at ca. 27° N, *I.M. Johnston 3654*, CAS, GH) and not at all from Sonora.

3. NICOLLETIA OCCIDENTALIS A. Gray in Frémont, Rep. exped. Rocky Mts. p. 316. 1845. Type: California, "banks of Mohahve river, growing in naked sands," Apr 1844, *Frémont "358"*. Holotype: NY!; isotypes: GH!, NY!

Perennials; strictly erect from deep taproots; 12—29 cm high; glaucous. Leaves at very base (soil level and below) reduced to scales, normal leaves 2—7 cm long, pinnately parted into 7—9 (5—11) short, patent or antrorse

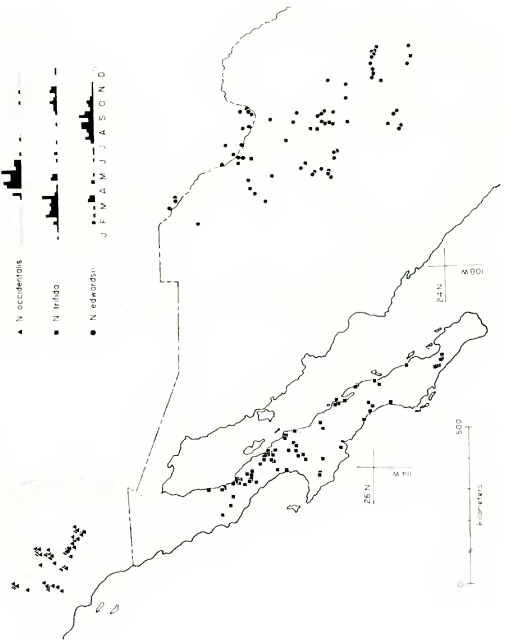

Fig. 1. Distributions of *Nicolletia* spp. Histograms indicate flowering times as determined from cumulative herbarium records.

lobes, fleshy and often crowded below the heads. Peduncles mostly 2—10 mm long, heads surpassed by foliage. Involucres broadly turbinate to cylindrical. Calyculus of 2—4 lanceolate to triangular bractlets 4—8 mm long. Phyllaries 8 (—12), linear to ovate, abruptly acute to acuminate, 14—18 mm long, 3.5—5.5 mm wide, somewhat fleshy, narrowly scarious-margined, often tinged with purple, each bearing 0—1 subapical and 0—4 submarginal glands. Ray florets 8—12; tube of corollas 5.5—6.5 mm long; laminae narrowly ovate-elliptic, 4.5—8.5 mm long, 2.5—3.8 mm wide; style branches exserted 2.8—3.8 mm. Disc florets (30—) 60—100+; corollas yellow, often tipped with purple, 8.2—9.5 mm long, tube 2.2—3.0 mm long, throat 4.8—5.5 mm long, lobes 0.8—1.1 mm long, deltoid, papillate, not glandular-puberulent; anthers 3.8—4.5 mm long including collar (0.4—0.5 mm long) and apical appendage (0.7—0.8 mm long); style branches 3.2—3.5 mm long, including appendage (0.9—1.2 mm long). Achenes 7—9 mm long. Pappus bristles 3—7 mm long; squamellae 6—8 mm long, including awn (1—2 mm long).

Distribution (Fig. 1): California, Mojave Desert from northeastern Kern Co. south into northeastern Los Angeles Co. and east and south across western San Bernardino Co. into north central Riverside Co. (Joshua Tree National Monument). Locally common in deep sands, often in floors of washes; 600—1400 m. Flowering mostly Apr—Jun, following winter rains (Fig. 1).

The often cited occurrence of *N. occidentalis* in San Diego Co., California, is apparently based on mislabelled specimens (*S.B. and W.F. Parish 193*). Some of these (GH, MO, US) read "sandy banks of Mojave River, May 1882." On others (DS, F, NY, PH, US), printed labels read "San Diego Co., San Felipe" and either May or June, 1882. Two of the latter have the printed locality struck through and "Mojave R" (NY) or "Mojave Desert" (US) written in. I have seen no other collections attributed to San Diego Co.

GEOGRAPHY

Distances separating geographic ranges of species pairs in *Nicolletia* are considerable: *edwardsii/occidentalis*—1000 km, *edwardsii/trifida*—650 km, and *occidentalis/trifida*—400 km (Fig. 1). Historical development of this distribution pattern invites speculation. The ancestral population of *Nicolletia* probably resided in central Mexico, center of diversity for Tageteae (Strother, 1977). But, how did *N. trifida* get to Lower California? How did *N. occidentalis* get to Mojave Desert? Long distance dispersal and colonization followed by differentiation in response to selection? Migrations of ancestral stock and subsequent differentiations and extinctions?

Comparative morphology of Nicolletias offers little help in reaching a conclusion, in making a choice between alternative hypotheses. No single species seems to be markedly more "primitive" or "archetypal" than the others. In *Dyssodia* subg. *Clomenocoma*, however, there is a group of species that form a definite, linear, morphological sequence from primitive to

advanced (Strother, 1969). Geographical distribution of this series of species has implications for interpreting the biography of *Nicolletia*.

In subg. *Clomenocoma*, *Dyssodia aurantia* and *D. appendiculata* are morphologically primitive and closely approximate a hypothetical archetype for *Dyssodia* in particular and Tageteae in general. *Dyssodia aurantia* is restricted to Veracruz; *D. appendiculata* ranges across southern Mexico from Chiapas to Colima. *Dyssodia squamosa* is closely related to *D. appendiculata* and ranges northwest of the latter from Jalisco through Nayarit into Sinaloa. Next in this series is *D. speciosa*, which is restricted to southern Baja California Sur. It is followed by *D. porophylloides*, which ranges from midpeninsular Lower California into California, Arizona, and Sonora. The series ends with *D. cooperi*, which ranges north from *D. porophylloides* in California and Arizona into southern Nevada (Strother, 1969). This morphological/geographical sequence in *Dyssodia* correlates closely with a continuum of increasing aridity of habitats (Walter and Lieth, 1967). *Dyssodia appendiculata* occupies rather mesic habitats and the habitat of *D. cooperi* is the most xeric of the series.

Nicolletias cannot be placed so readily into a linear evolutionary sequence, nor do they cover such a broad spectrum of habitats. Still, a history of migration from the Chihuahuan Desert region into the Sonoran and Mojave deserts followed by differentiations and extinctions seems to be a plausible explanation for present distributions of these species.

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